MORPHOLOGY AND PHYLOGENETIC INFORMATIVENESS OF EARLY ARCHOSAUR BRAINCASES

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ABSTRACT. The braincases of the Triassic early archosaurs *Vjushkovia triplicostata*, *Fugusuchus hejiapensis*, *Xilousuchus sapingensis*, and *Shansisuchus shansisuchus* are described in detail for the first time. A preliminary analysis investigating the phylogenetic informativeness of braincase morphology in the earliest archosaurs incorporates 11 archosauromorph taxa and 17 informative characters. A further seven uninformative and eight problematical braincase characters are discussed. Parsimony and character compatibility permutation tests suggest at the highest possible confidence levels that the data set contains significant hierarchical structure, interpreted as the result of phylogeny. The most parsimonious tree based only on braincase data agrees broadly with existing ideas of early archosaur relationships. However, it conflicts with recently published hypotheses in a number of details, most notably in the presence of a holophyletic Proterosuchia and a well-supported clade of *Erythrosuchus* + *Shansisuchus*. The use of *Prolacerta* as an outgroup does not perturb the parsimonious interpretation of relationship of the included early archosaurs. Topological constraints and additional analyses performed on subsets of the 11 taxa show that some of the hypothesized relationships based only on braincase data are not robust. Unremarkable consistency indices and weakly supported relationships suggest that braincase morphology does not represent an especially informative source of data for the reconstruction of earliest archosaur phylogeny, although this remains an area for further investigation.

ARCHOSAURIA is a major group of diapsids that includes the crocodiles, birds, dinosaurs, pterosaurs, and less well-known forms that together dominated the aerial and terrestrial large vertebrate niches for virtually the whole of the Mesozoic. Understandably, the phylogeny of such a major radiation has attracted considerable attention. All of the many recent studies of the phylogeny of the basal archosaurs (e.g. Gauthier 1986; Benton and Clark 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1992, 1993) have excluded some of the more poorly understood earliest forms, and treated the remainder only briefly. Lack of descriptive information for early archosaurs is exemplified by our current knowledge of braincase morphology in these taxa. Indeed, braincase morphology often remains poorly known even in the more derived and generally better understood archosaurs. By virtue of its intricate structure, large number of components, and perceived partial separation from the more obviously functionally adapted parts of the skull, the braincase has been considered to represent perhaps an especially important source of phylogenetic information (e.g. Gow 1975; Parrish 1993). This may be especially true for the early archosaurs, a great number of which have tall, laterally compressed, and superficially similar carnivorous skulls (Gauthier 1986; Parrish 1993).

The aim of this paper is to provide detailed osteological descriptions of the braincases of four poorly known early archosaurs: *Vjushkovia triplicostata*, *Fugusuchus hejiapensis*, *Xilousuchus sapingensis* and *Shansisuchus shansisuchus*. These forms are representatives of the Proterosuchia, a group that includes the very earliest archosaurs and which, upon current understanding (e.g. Benton and Clark 1988; Parrish 1992, 1993), is a paraphyletic grouping of the Proterosuchidae and Erythrosuchidae. The braincase descriptions presented here are based on the thorough observation of original specimens. They are followed by a preliminary attempt to investigate the informativeness of the phylogenetic data that braincase morphology yields. The braincase of *Erythrosuchus* will be

described in detail elsewhere, as will be the endocranial casts of *Erythrosuchus*, *Vjushkovia triplicostata* and *Xilousuchus* (Gower and Sennikov in press).

The taxon Archosauria is applied throughout in its traditional concept, rather than in the crown-group concept advocated by Gauthier (1986). The taxa in the less inclusive Archosauria of Gauthier (1986) are here referred to as 'crown-group archosaurs'.

The abbreviations used for institutional collections are as follows: BMNH, The Natural History Museum, London; BPI, Bernard Price Institute for Palaeontological Research, Johannesburg; GMB, Geological Institute, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; PIN, Paleontological Institute of the Russian Academy of Science, Moscow; UMCZ, University Museum of Zoology, Cambridge.

DESCRIPTIVE ACCOUNTS

Vjushkovia triplicostata *von Huene* (Text-figs 1–3)

Vjushkovia triplicostata is an erythrosuchid from the Yarenga Gorizont (upper part of the Lower Triassic) from the southern Urals of European Russia. It was originally described by von Huene (1960), who studied a syntypic series of specimens from a single site (now a lectotype and many paralectotypes; see Charig and Sues 1976). Von Huene's brief description included only a superficial treatment of the braincase, and comparison with known early archosaurs was minimal. Since the original description, Parrish (1992) has figured part of the braincase of PIN 951-60 and scored *V. triplicostata* for three braincase characters, and Clark *et al.* (1993) have briefly documented the presence and general form of the ossified laterosphenoid. Parrish (1993, fig. 2) has also sketched the route of the internal carotid artery.

The following braincase description and all of the figures are based on the most complete and best preserved specimen, paralectotype PIN 951-60. Information was also obtained from the lectotype PIN 951-59.

Basioccipital. The basioccipital forms most of the occipital condyle and its dorsolateral corners are excavated to receive the exoccipitals. Posteriorly, it is exposed for a small area on the floor of the foramen magnum, but further forward any exposure on the floor of the main part of the braincase is prevented by midline contact between the overlying exoccipitals. The notochordal pit (Text-fig. 2A) and condylar 'neck' (Text-fig. 2B) are clearly visible.

The basal tubera of the basioccipital are relatively small, simple, and ventrally projecting, and are separated by a smaller, medially positioned tubercle (Text-fig. 1). This is contrary to the information presented by Parrish (1992), who mistakenly identified the ventral rami of the opisthotics as lateral components of the basal tubera of the basioccipital, and listed this as an erythrosuchid synapomorphy (Parrish's character 9). We have observed a clear line of contact between the posterior surface of these two elements.

Exoccipital. The exoccipitals meet anteriorly along the midline to exclude the basioccipital from the floor of the endocranial cavity. Posteriorly their medial margins diverge, allowing the basioccipital to form part of the ventral border of the foramen magnum (Text-fig. 2A). At the base of each exoccipital 'pillar' is a single opening for the hypoglossal nerve (XII). Here the exoccipital forms the posterior border of the metotic foramen. The posterodorsal suture with the opisthotic cannot be discerned, although it is probably the exoccipitals which form the majority of the dorsal part of the border to the foramen magnum.

Supraoccipital. The supraoccipital is a shield-like element, excluded from the border of the foramen magnum by dorsomedial contact between the exoccipitals. The posterodorsal surface of the supraoccipital is markedly rugose and the sutures with the parietal, postparietal, and paroccipital process are all simple.

Opisthotic. The opisthotic forms most of the paroccipital process, which has an expanded, angular end with a distal notch. Articulation with the parietal is similar to that in *Erythrosuchus*, with a ventral parietal socket articulating with a dorsal paroccipital projection. The dorsal margin of the paroccipital process lies close to the ventral margin of the parietal, suggesting that the posttemporal fenestra was significantly reduced. The medial end of the posterior surface of the paroccipital process bears a well-defined depression. Within the well-developed stapedial groove the lamellar part of the ventral ramus of the opisthotic separates the metotic
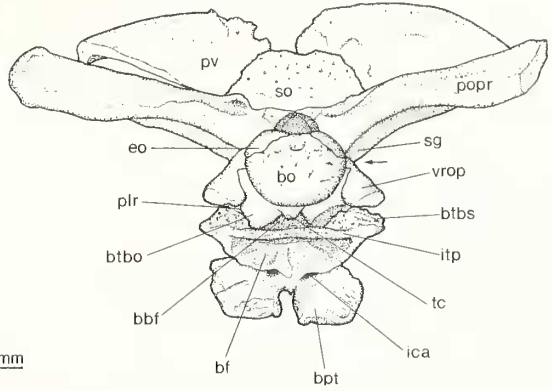
TEXT-FIG 1. *Vjushkovia triplicostata*. Photograph and drawing of posterior and slightly ventral view of braincase of PIN 951/60. Arrow marks main line of fracture dividing specimen into dorsal and ventral portions.
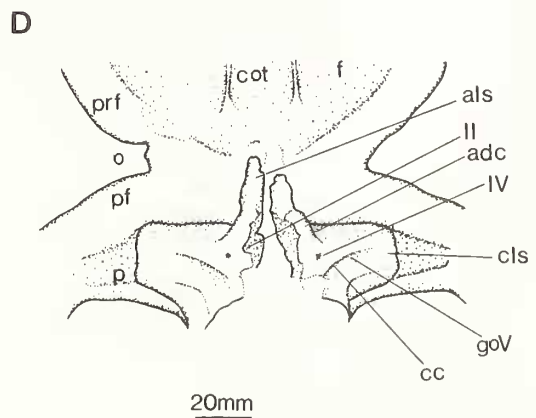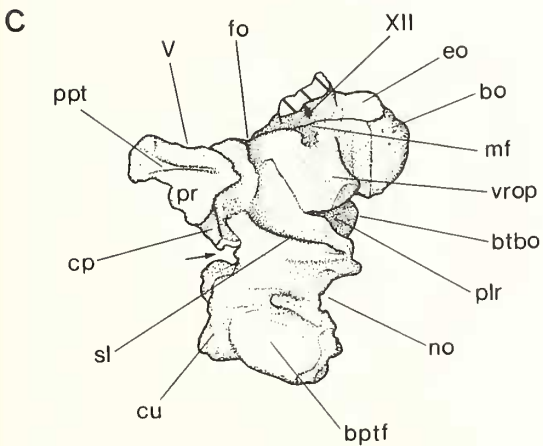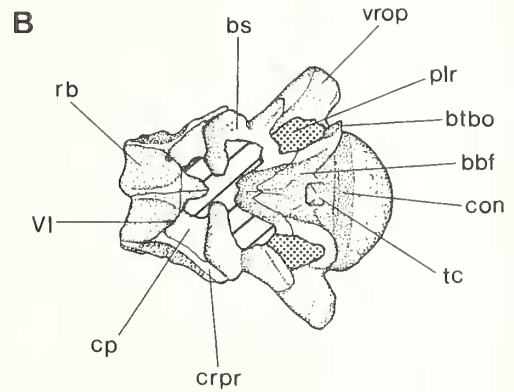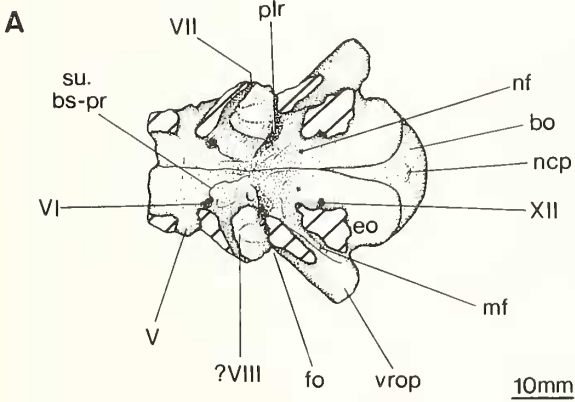
TEXT-FIG 2. *Vjushkovia triplicostata*. A–C, Braincase of PIN 951/60. A, dorsal view of ventral portion, i.e. region below arrow in Text-figure 1. B, ventral view along line of fracture indicated by arrow in C. C, left lateral view. D, ventral view of laterosphenoids and posterior of the skull roof of PIN 951/59.

foramen from the fenestra ovalis. The ventral ramus extends ventrally to form a rounded and dramatically expanded distal end. This stands proud of the crista prootica and is clearly visible in lateral (Text-fig. 2B) and occipital (Text-fig. 1) views. Situated between the distal end of the opisthotic ramus and the dorsal surface of the lateral part of the basisphenoid is an anterodorsally extending channel of unknown function (see below).

Prootic. The posterior part of the prootic forms the anterior face of the proximal end of the paroccipital process. Further anteriorly, the prootic forms a large part of the lateral wall of the braincase and holds the foramen for the exit of the trigeminal nerve (V). Exclusion of the laterosphenoid from the border of the trigeminal foramen is probable, but not certain. A thin but well-defined horizontal ridge is located beneath the simple border of the trigeminal foramen. The crista prootica is not simply curved, but is instead sinusoidal (Text-fig. 2C). The posterior part of this edge, at a point posterior the end of the horizontal ledge described above, holds the apparently single exit foramen for the facial nerve (VII).

The inferior anterior process of the prootic extends forwards for some distance beyond its articulation with the clinoid process of the basisphenoid, before articulating with the laterosphenoid. This freestanding part of the prootic presents a largely ventrally directed surface which holds the exit foramen for the abducens nerve (VI). This foramen lies within a fossa that probably represented the attachment site of the retractor bulbi eye muscles.

Basisphenoid. The basisphenoid of *V. triplicostata* is similar to that of *Erythrosuchus* in being tall and longitudinally short, and in exhibiting a vertical rather than horizontal alignment of the basal tubera and basipterygoid processes. Additionally, the lateral surface of the basipterygoid process and basal tuber are similar in area (Text-fig. 2B). There is little lateral sheathing of the basioccipital by the posterodorsal part of the basisphenoid, because of the presence of the large clubbed end of the ventral ramus of the opisthotic. The posterior edge of the clinoid process harbours a deeply incised groove, which would have transmitted the palatine branch of the facial nerve to a notch between the basisphenoid tuber and the basipterygoid process, which it would have passed through together with the internal carotid artery. The basipterygoid process bears an anterolaterally directed, oval facet with a prominent ridge above its posterodorsal end.

The lateral face of the basal tuber is more irregular in form. Anterodorsally it is overlapped by the crista prootica, while posterodorsally it forms a clearly defined contact with the ventral ramus of the opisthotic. The main part of the lateral face of the tuber is dominated by an anteroventrally bordered, curved, and gutter-like groove. This extends from beneath the crista prootica to the posterior edge of the tuber (the dorsal part of this channel is incomplete in PIN 951-60; Text-fig. 2C), and is interpreted as a strongly developed homologue of the 'channel' seen in a similar position on the basisphenoid of *Prolacerta* (termed 'semilunar depression' by Evans 1986).

The posterior surface of the basisphenoid (Text-fig. 1) is complex. The upper surface of the basal tubera are highly rugose and they make simple contact briefly with the ventral rami of the opisthotics and the basal tubera of the basioccipital. A strong horizontal plate extends between the tubera of the basisphenoid, a feature considered to be an erythrosuchid synapomorphy by Parrish (1992, character 10), and referred to here as the 'basisphenoid intertuberal plate'. This plate is emphasized in that it forms the dorsal border to a deep, funnel-shaped fossa, referred to here as the 'basisphenoid fossa'. The dorsal margin of the plate forms a crevice-like concavity with the ventral edges of the basal tubera of the basioccipital. This is referred to here as the 'basioccipital-basisphenoid fossa'. The ventrolateral margins of the basisphenoid fossa are delineated by a second ridge, or more accurately a pair of ridges that do not quite meet along the midline. The ventral edges of these paired ridges harbour the foramina which transmitted the cerebral branches of the internal carotid arteries, from the notches between the basal tubera and basipterygoid processes to the pituitary fossa. The palatine branches of the internal carotid arteries and facial nerves would have branched off outside these foramina to pass anteriorly to a ventral notch between the two basipterygoid process. From here they would have continued forward, with the left and right pairs of the nerve and vessel being separated by a low ventral keel. In Parrish's (1993) figure 2A, the feature labelled 'Bp' is not the basipterygoid process, but rather the basal tuber of the basisphenoid.

The parasphenoid is indistinct suturally from the basisphenoid. The rostrum/cultriform process is incomplete in both PIN 951-59 and 951-60. Its base can be seen between the anterior ends of the basipterygoid processes of the basisphenoid (Text-fig. 2C). The base is tall and laterally compressed, with a ventral edge that is virtually level with the ventral edge of the basipterygoid processes.

Laterosphenoid. Clark *et al.* (1993) were the first to record the presence of a laterosphenoid ossification in *V. triplicostata.* This element is also apparent from Tatarinov's (1961) figure 3, despite being identified as an
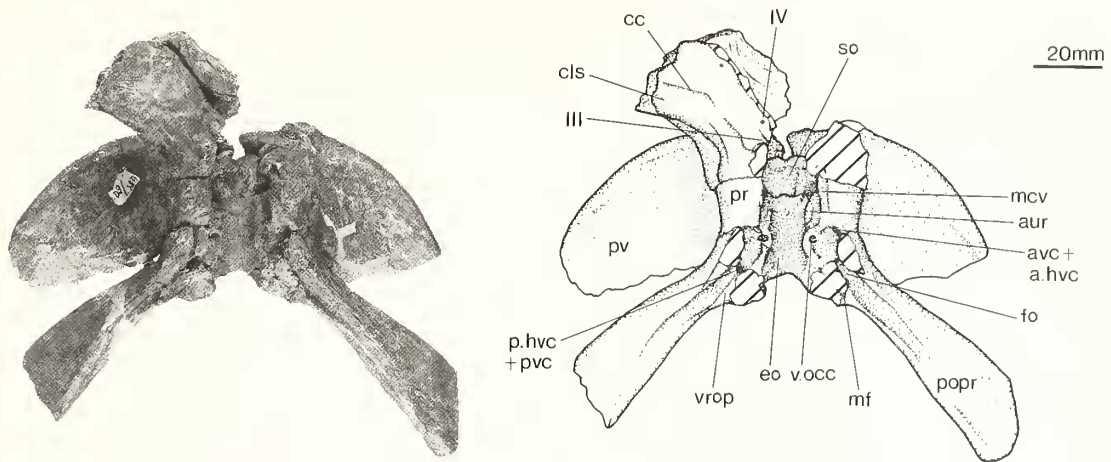
TEXT-FIG 3. *Vjushkovia triplicostata*. Photograph and drawing of ventral view of dorsal portion of braincase of PIN 951/60.

anterior extension of the prootic. Contrary to the statement by Clark *et al.*, the examples in which laterosphenoids are preserved are PIN 951/59 (lectotype, see Charig and Sues 1976; Parrish 1992) and 951/60 (paralectotype). Both of these specimens are dorsoventrally crushed. 951/60 (Text-fig. 3) has lost the anterior processes, and both specimens are ventromedially incomplete. The capitate process bears a strong lateral ridge and a more anterior cotylar crest (Clark *et al.* 1993). A groove lying immediately posterior to this crest would probably have carried the ophthalmic branch of the trigeminal nerve in an anterodorsal direction away from the trigeminal foramen. There is no sign of an epipterygoid pit dorsally, but poor preservation of this area, especially in 951/60, means that this requires verification. The erosion of most of the ventromedial edge in both specimens has made the identification of the position of the exit of the optic (II) and oculomotor (III) nerves difficult. They probably passed through notches seen on the ventromedial edges of the laterosphenoids of 951/59 (Text-fig. 2D), in a position similar to those in *Proterosuchus* and *Erythrosuchus*. A small foramen for the exit of the trochlear nerve (IV) is seen in a position above and lateral to this. The anterior process of the laterosphenoid is longer and more slender than those of *Erythrosuchus*, but without approaching the dimensions seen in *Proterosuchus* (Clark *et al.* 1993). The concavity on the skull roof for the capitate process seems to extend onto the postorbital, but as preserved there is no direct evidence of postorbital-laterosphenoid contact. This area of the specimen is partly repaired and sutures are hard to identify. PIN 951/59 shows that an anterodorsal channel between the parietal and the capitate and anterior processes of the laterosphenoid was present.

As a result of the almost horizontal fracture of specimen PIN 951-60, information can also be presented on the internal surface of the braincase.

Ventral surface (Text-fig. 2A). The basioccipital is exposed on the floor of the posterior part of the foramen magnum as a result of the divergence of the medial margins of the exoccipitals. Further anteriorly the exoccipitals meet along the midline. A single internal foramen where the hypoglossal nerve exited can be seen at the base of each exoccipital pillar. Medial to the anterior margin of the pillars, there is a single pair of nutrient foramina on the floor of the braincase. Just in front of this, the exoccipital slopes down towards the main part of the endocranial cavity. The suture between the exoccipital and opisthotic can be seen on the floor of the metotic foramen, between the front of the pillar and the sectioned ventral ramus of the opisthotic (Text-fig. 2A). The fenestra ovalis is less clearly defined, but lies immediately in front of the ventral ramus of the opisthotic, its anteroventral margin formed by the basisphenoid. The basisphenoid forms most of the central part of the braincase floor. Although the entire course of the exoccipital-opisthotic suture is not discernible, it is certain that medial exposure is not achieved by the basisphenoid. This permits a little prootic-exoccipital contact medially. The basisphenoid forms at least the ventral and posteroventral borders to the channel that carried the facial nerve on a posterolateral route out through the braincase wall.
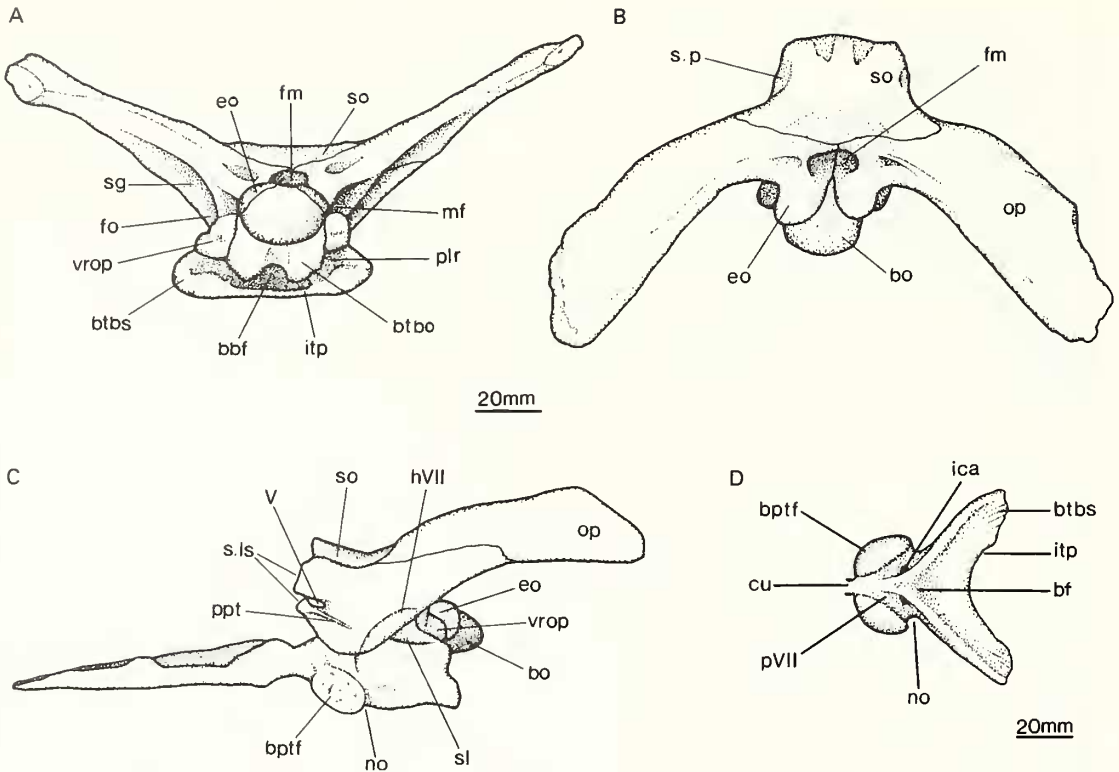
TEXT-FIG 4. *Fugusuchus hejiapensis*. Braincase of GMB V313 without laterosphenoid. A, posterior and slightly ventral, B, dorsal and C, left lateral views. D, ventral view of basisphenoid.

Immediately behind the posterior wall to the facial nerve channel, the basisphenoid slopes back and down to form a slightly cup-shaped anteroventral border to the largely unossified inner ear region. At the posteroventral limit of this part of the basisphenoid, just inside the fenestra ovalis and along the suture with the exoccipital, there is a crevice running parallel to the facial nerve channel. This crevice, although currently not fully prepared, extends ventrally for a short distance, and would appear to be in a position where an ossified lagenar (cochlear) recess might be found. This area of the braincase floor appears similar to that described for *Plateosaurus* by Galton (1985). There is doubt about identifying this as a lagenar recess because of its absence in *Erythrosuchus*, and the fact that this recess in *V. triplicostata* is weakly defined and continues posteriorly to open out on the occipital surface of the braincase, between the ventral ramus of the opisthotic and the basal tubera of the basioccipital and basisphenoid. Equivalent posterior openings are also seen in, for example, *Proterosuchus* (labelled fenestra ovalis by Broili and Schröder 1934, fig. 6) and *Prolacerta* (Gow 1975, fig. 34). Although an ossified recess is known in crown-group archosaurs, it is only known to be elongated in a restricted group of taxa including birds, crocodiles and dinosaurs (see Walker 1990, p. 111, for a fuller discussion), and in these forms it remains a blind hollow. It is possible that the channel in these plesiomorphic taxa considered here represents an area of residual cartilage, particularly as it is present as a gap between a number of elements that is closed in some closely related taxa. It is here termed the 'pseudolagenar recess'.

Most of the rather flat anterior end of the braincase floor is formed by the prootics which meet along the midline. The abducens foramina pass through the braincase floor from between the trigeminal and facial foramina. While the external abducens foramina are entirely within the prootic, their internal counterparts are positioned on the prootic-basisphenoid commissure.

Dorsal surface (Text-fig. 3). The supraoccipital forms only the anterior part of the ceiling to the endocranial cavity. The exoccipitals form most of the ceiling, although a midline suture between them is not visible.

Posterolaterally, the vestibule is present as a well-defined hollow, the upper part of which holds three unprepared foramina. One is positioned near the broken surface and lies at the posterior limit of the vestibule, interpreted as the posterior opening of the horizontal (or external) and posterior vertical semicircular canals. The posterior ampulla would also have been positioned here. The second opening lies at the same height as this, but in the anterolateral corner of the vestibule. This would have led to the ventral opening of the anterior vertical canal and the anterior opening of the horizontal canal, and would also have held the anterior and external ampullae. The third foramen is situated in the dorsal surface of the vestibule and is interpreted as the ventral limit of the osseus common crus. The medial wall of the otic capsule is not ossified and there is no sign of a foramen perilymphaticum. The auricular recess lies on the medial surface of the thickened wall of the prootic in front of the vestibule. Curving around the dorsal and anterior perimeter of this recess is a groove for the middle cerebral vein, which would have passed through the braincase wall via the trigeminal foramen.

Positive identification of foramina for the acoustic nerve has not been possible. This may be the result of the loss of bone along the line of fracture between the dorsal and ventral parts of the braincase of PIN 951-60, as well as incomplete preparation, but also possibly because they were not ossified. However, a small notch seen immediately outside the anterodorsal limit of the 'pseudolagenar recess' may be a candidate for a possible branch of the acoustic nerve.

## Fugusuchus hejiapanensis *Cheng* (Text-fig. 4)

Fugusuchus hejiapanensis is currently known from a single, incomplete specimen (GMB V 313) from the Heshanggou Formation (upper part of the Lower Triassic) of China. It was originally described by Cheng (1980), who identified this taxon as a proterosuchid. He presented only brief notes on the braincase along with a few incompletely labelled diagrams and some unlabelled photographs. Parrish (1992), who postulated that *Fugusuchus* is the most plesiomorphic member of a holophyletic Erythrosuchidae, scored it for three braincase characters but provided no discussion. A redescription of the braincase of *Fugusuchus* is presented here, together with new figures.

The holotype has a well-preserved braincase, free form the rest of the skull and easily studied in three dimensions. The laterosphenoid, preserved but separated from the rest of the braincase (also reported for the early archosaurs *Proterosuchus* and *Euparkeria* by Clark *et al.* 1993), was unfortunately unavailable for examination at the time of this study. There is a slight distortion and relative sliding of some of the elements. Very little detail of descriptive merit could be obtained from the internal surface of the braincase.

Basioccipital. The basioccipital forms most of the condyle, which is fairly elongate when compared with that of other early archosaurs. The basal tubera are a pair of broad, flat, and simple ventral projections that are separated by a shallow, central groove. They do not extend laterally, but instead make contact with the medial edges of the distal ends of the ventral rami of the opisthotics (Text-fig. 4). This is contrary to the description by Parrish (1992), who recorded *Fugusuchus* as having lateral and ventral components to the basal tubera of the basioccipital. As with *V. triplicostata*, he appears to have mistakenly identified the ventral rami of the opisthotics as lateral components of the basal tubera of the basioccipital, when in fact a line of contact is observable between these elements posteriorly. The basioccipital is exposed on the floor of the foramen magnum, but makes no contribution to the ventral surface of the main part of the cerebral cavity.

Exoccipital. The medial margins of the exoccipitals diverge posteriorly on the floor of the foramen magnum, partly exposing the basioccipital (Text-fig. 4B). They meet anteriorly, however, to exclude the basioccipital from the floor of the main part of the braincase. The opposite exoccipitals meet above the foramen magnum, excluding the supraoccipital from the dorsal border of this opening. There is no indication of a suture between the exoccipitals and the opisthotics at the bases of the paroccipital processes. There are well-defined concavities present in this area, just as described above for *V. triplicostata* above. Only one external opening for cranial nerve XII can be seen on the exoccipital, where it forms the posteromedial wall of the metotic foramen.

Supraoccipital. The supraoccipital is a simple shield of bone excluded from the border of the foramen magnum. There are two small V-shaped depressions on the anterior edge of the dorsal surface. The anterolateral part of the supraoccipital, immediately above the point of contact with the prootics, bears facets for articulation with the parietal (Text-fig. 4B).
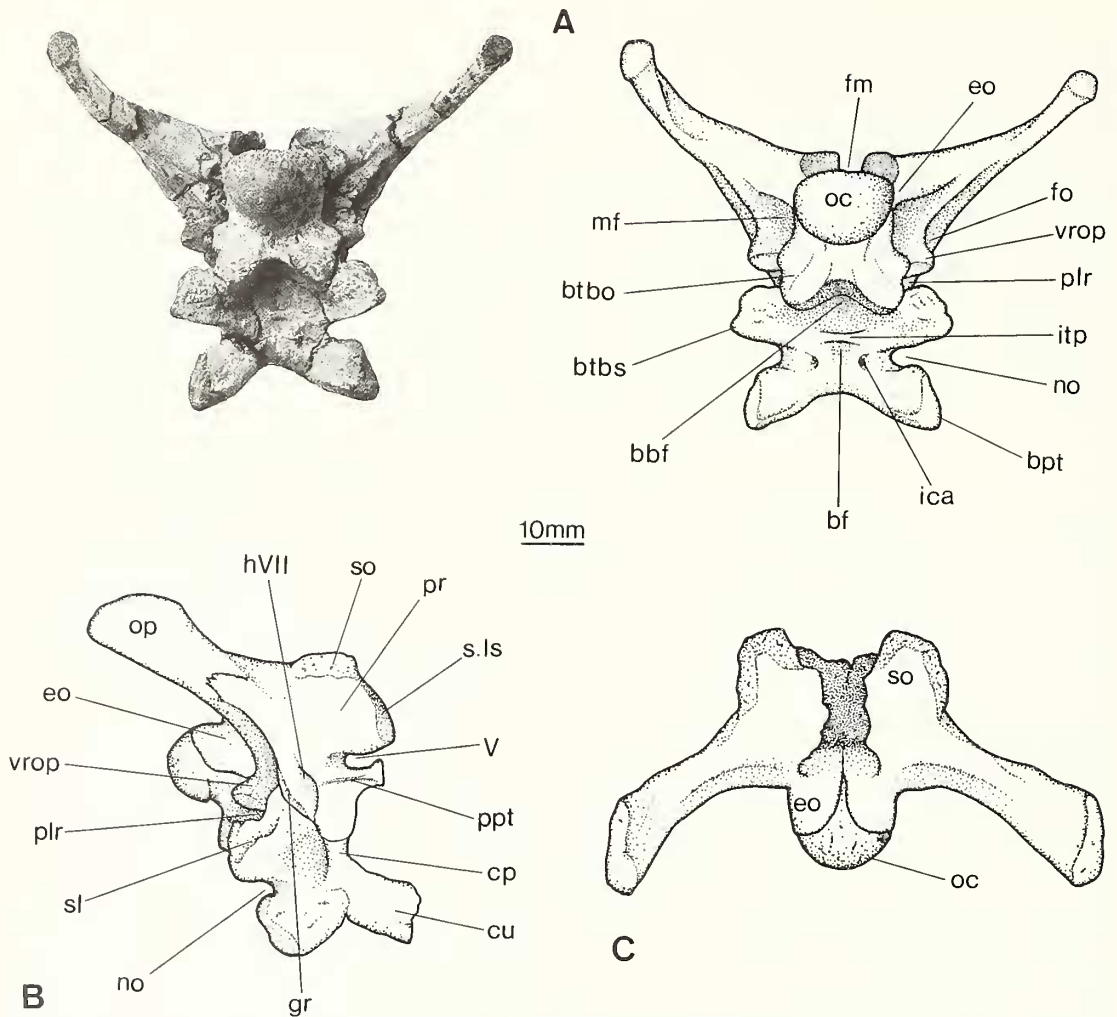
TEXT-FIG 5. *Xilousuchus sapingensis*. Braincase of IVPP V6026. A, posterior and slightly ventral, B, right lateral and C, dorsal views.

Opisthotic. The opisthotic forms most of the flat and broad paroccipital process. There is no prominent dorsal process for articulation with the ventral surface of the parietal, although the posttemporal fenestra still seems to have been reduced to what was, at most, a narrow slit. The ventral ramus of the opisthotic is very well developed, stands proud of the crista prootica, and is clearly visible in posterior (Text-fig. 4A) and lateral (Text-fig. 4C) views. The distal end is rounded and greatly expanded.

Prootic. The prootic forms a substantial part of the lateral face of the braincase. The trigeminal foramen is somewhat crushed, so that the observed suggestion of a laterosphenoid contribution perhaps requires confirmation. The lateral surface of the superior anterior process is featureless, while the inferior anterior process bears a thin horizontal ridge, equivalent to that described for *V. triplicostata*. The margin of the crista prootica follows a regular and simple curve. Near the posteroventral part of the crista prootica, the lateral face of the prootic bears a curved groove which harbours the foramen for the facial nerve. The posterodorsal part of the groove indicates the former path of the hyomandibular branch of the facial nerve, while the anteroventral end was for the palatine branch. The groove for the palatine branch reaches the margin of the

crista prootica, while the hyomandibular branch groove falls just short. The process below the trigeminal foramen has a ventrally facing surface which holds the depression in which the abducens foramen was situated. This area of the braincase is less well preserved, with neither the abducens foramina nor the prootic-basisphenoid suture being detectable.

Basisphenoid. The overall form of the basisphenoid is reminiscent of that of *Proterosuchus* (Cruickshank 1972; Gow 1975), but is unlike that of *V. triplicostata* and *Erythrosuchus*, in that it is horizontally aligned and plate-like. The basipterygoid processes are in front of, rather than below the basal tubera. Additionally, the lateral surface areas of the basal tubera are greater than those of the basipterygoid processes (Text-fig. 4c).

Posterodorsally, the lateral faces of the basal tubera bear semilunar depressions, apparently homologous with, but less incised than, those described above for *V. triplicostata*. The clinoid process of the basisphenoid is not particularly well defined. Its posterior margin harbours a groove that would probably have carried the palatine branch of the facial nerve to the notch between the basal tuber and basipterygoid process.

In ventral view (Text-fig. 4d), the plate-like form of the basisphenoid and its similarity to that of *Proterosuchus* and *Prolacerta* can clearly be seen. Posteriorly, the basal tubera diverge strongly. Between the posterior edge of the basal tubera is a curved plate of bone, homologous to the basisphenoid intertuberal plate described above for *V. triplicostata*. Anteriorly, the approximately hemispherical basipterygoid processes and facets can be seen, with the base of the cultriform process extending from between them anteriorly. The paired foramina for the cerebral branches of the internal carotid arteries are positioned ventrally and between the posterior ends of the basipterygoid processes. These foramina are separated along the midline by a ridge that extends forwards and separated the left and right sides of the palatine branches of the facial nerve and internal carotid arteries, right up to the base of the cultriform process of the parasphenoid. The posterior end of this ridge bifurcates, with both branches extending backwards along the anterolateral ventral edges of the basal tubera. This Y-shaped ridge is equivalent to the paired ridges over the carotid foramina of *V. triplicostata*. In *Fugusuchus* the posterior edges of the two branches of this divided ridge form the anterior limit to a concavity on the ventral surface of the basisphenoid, homologous to the funnel-shaped basisphenoid fossa described above for *V. triplicostata*. Despite being a horizontally, rather than more vertically aligned basisphenoid, the arrangement of the ridges and fossae in *Fugusuchus* is essentially the same as that seen in *V. triplicostata*.

In posterior view, the intertuberal plate can be clearly seen. It forms the basioccipital-basisphenoid fossa in conjunction with the basal tubera of the basioccipital. The external opening of the 'pseudolagenar recess' is seen as a narrow hollow between the dorsal surface of the basisphenoid, the ventral edge of the basal tuber of the basioccipital, and the ventral ramus of the opisthotic.

The cultriform process of the parasphenoid is essentially complete. It can be seen in lateral view (Text-fig. 4c) that it tapers smoothly along its length, except for a constriction near its base. The process is U-shaped in transverse section, and has a pointed distal end. The base bears weakly developed lateral grooves that probably indicate the former path of the palatine branches of the facial nerve and internal carotid artery. The parasphenoid is indistinct suturally from the basisphenoid.

Xilousuchus sapingensis *Wu* (Text-fig. 5)

Xilousuchus sapingensis, known from fragmentary skull and postcranial material from the Heshanggou Formation (upper part of the Lower Triassic) of China, was originally described by Wu (1981) as a proterosuchid. This taxon has been ignored in all of the recent cladistic analyses of basal archosaur phylogeny. The known braincase material is part of a unique specimen, the holotype IVPP 6026. It is disarticulated from the rest of the very incompletely preserved skull. External preservation is good, but fine detail has not been preserved and/or prepared internally, and the laterosphenoid is absent/missing. Wu (1981) described and figured the braincase briefly and compared it with that of *Proterosuchus*. Corrections, further details and comparisons, and new figures are presented here.

Basioccipital. The basioccipital is a short element closely resembling that of *V. triplicostata*, *Fugusuchus* and *Proterosuchus* (Cruickshank 1970) in that the exoccipitals prevent it from contributing to the anterior part of the braincase floor, but is exposed further posteriorly on the floor of the foramen magnum. The basal tubera are large, bilobed, strongly diverging, and separated by a broad notch (Text-fig. 5a). The ventral surface of the basal tubera of the basioccipital contribute to the basioccipital-basisphenoid fossa, which is larger than in the other taxa described here.

Exoccipital. Anteroventrally, the medial margins of the exoccipitals meet along the midline, but posteriorly they diverge (Text-fig. 5c). The dorsal part of the exoccipital is indistinct suturally from the opisthotic. The dorsal border of the foramen magnum is incomplete, leading to uncertainty over whether or not the exoccipitals meet along the midline to exclude the supraoccipital from its border. A relatively large area of the lateral surface of the exoccipital is exposed, and there is a single opening for the hypoglossal nerve.

Supraoccipital. The supraoccipital is firmly attached to the rest of the braincase and its suture with the base of the paraoccipital process cannot be detected. The central part of the supraoccipital is missing, so that the possibility of contribution to the dorsal border of the foramen magnum, or to an occipital peg, is currently unknown.

Opisthotic. The opisthotic forms most of the paroccipital process, which has an expanded, rounded, and unnotched distal end. There is no indication of a process on the dorsal edge of the paroccipital process which might have articulated with the ventral surface of the parietal (as seen in *Erythrosuchus* and *V. triplicostata*). Posteromedially, the bases of the paroccipital processes are shallowly concave, but the depressions are not as well defined as in *V. triplicostata* or *Fugusuchus*.

Between the metotic foramen (which probably would have transmitted cranial nerves IX, X, XI, and not X, XI, XII as suggested by Wu 1981) and the fenestra ovalis, the ventral ramus of the opisthotic projects downwards and ends distally in a much expanded, club-like tip. This stands proud of the crista prootica and is clearly visible in posterior and lateral views. The distal end of the ventral ramus of the opisthotic is surrounded by three openings: the fenestra ovalis and metotic foramen above, and the posterior opening of the 'pseudolagenar recess' below. Posteriorly, the ventral ramus of the opisthotic articulates with the basal tubera of the basioccipital, while anteriorly its base is sheathed laterally by the basisphenoid.

Prootic. The posterior part of the prootic forms the anterolateral surface of the base of the paroccipital process, its suture with the opisthotic being not entirely clear. The rest of the prootic forms much of the lateral face of the braincase (Text-fig. 5b). The dorsal area of the lateral face of the prootic bears an anteroventral-posterodorsal groove, which widens and deepens posteriorly. This may be associated with the posttemporal fenestra.

The trigeminal foramen would have been formed by the laterosphenoid (if present) as well as the prootic. The lateral surface of the superior anterior prootic process is smooth and featureless. The inferior anterior process is much smaller, has an upturned anterior end, and bears a thin horizontal ridge on its lateral surface. Immediately behind the trigeminal foramen is a well-defined and posteriorly directed concavity of unknown function. The anterior surface of both of the anterior prootic processes are roughened and would have articulated with the laterosphenoid (if present). The ventral surface of the inferior process holds downward-facing concavities, in which the prootic forms the entire border of the abducens exit foramen. This is contrary to Wu's (1981) description of the position of the abducens foramina as within the basisphenoid.

The foramen for the facial nerve lies within a curved groove behind and below the trigeminal opening. The posterodorsal end of the groove (for the hyomandibular branch of the facial nerve) dies out on the lateral prootic surface, while the ventral part (palatine branch) continues to the posteroventral edge of the crista prootica. The crista prootica is like that of *V. triplicostata* in being sinusoidally curved. Part of its edge carries a fine groove, extending between the stapedial groove and the groove for the palatine branch of the facial nerve.

Basisphenoid. The basisphenoid of *Xilousuchus* forms a large part of the braincase. It is essentially a vertically aligned element and, viewed laterally (Text-fig. 5b), the basal tubera and basipterygoid processes are of similar size. The dorsal limit of the basal tuber extends up between the crista prootica and the distal end of the ventral ramus of the opisthotic. Its lateral face bears the semilunar depression, which is not particularly strongly incised, and is perhaps unusual in being sinusoidal, running parallel to the dorsal border of the basal tuber.

Between the basal tuber and the basipterygoid process there is a well-developed notch for the passage of the internal carotid artery and palatine branch of the facial nerve. The basipterygoid facet is sub-triangular. Anterodorsally, the basisphenoid forms a well-defined clinoid process that articulates with the anteroventral edge of the prootic. Its posterior edge forms the anterior margin of a deep depression that meets the two grooves on the edge of the crista prootica, described above. This depression curves back and becomes shallower, and its anterior margin probably would have harboured the palatine branch of the facial nerve on its way to the notch between the basal tuber and basipterygoid process. Although relatively large and deeply

incised, this depression does not hold a foramen for the passage of the cerebral branch of the internal carotid artery as described by Wu (1981); rather this foramen is on the posteroventral surface of the basisphenoid. Deep depressions on the lateral surface of the basisphenoid of some more derived archosaurs may be associated with pneumatic recesses of the tympanic cavity (see e.g. Chatterjee 1991).

In posterior view, the ventral ramus of the opisthotic is seen not to make substantial contact with the dorsal surface of the basal tubera of the basisphenoid, and the resultant gap forms the external opening of the 'pseudolagenar recess'. The basisphenoid intertuberal plate is only weakly developed. The basisphenoid fossa below it is considerably smaller and shallower than the basioccipital-basisphenoid fossa above it. Low, paired ridges that extend a short distance medially from the posteroventral edges of the basal tubera in the direction of the internal carotid foramina, represent the equivalent of the medially incomplete second ridge in *V. triplicostata* and the Y-shaped ridge in *Fugusuchus*. The foramina carrying the cerebral branches of the internal carotid arteries to the pituitary fossa are positioned posteriorly, close to the notches between the basipterygoid processes and basal tubera of the basisphenoid. The path of the palatine branches of the internal carotid artery and facial nerve is not well defined. There is, apparently, no ventral keel separating the left and right pairs of these elements. The posterior and ventral edges of the basipterygoid processes are noticeably thickened.

The parasphenoid is suturally indistinct from the basisphenoid. The cultriform process of the holotype is incomplete. The proximal end is not particularly deep, so that it is not confluent with much of the anterior edge of the clinoid process of the basisphenoid. There is no indication of the proximal constriction that is seen in *Fugusuchus*. The transverse section is V-shaped. Posteriorly, at the base, the dorsal surface shows a well-defined pituitary fossa housing the anterior foramina for the internal carotid arteries.
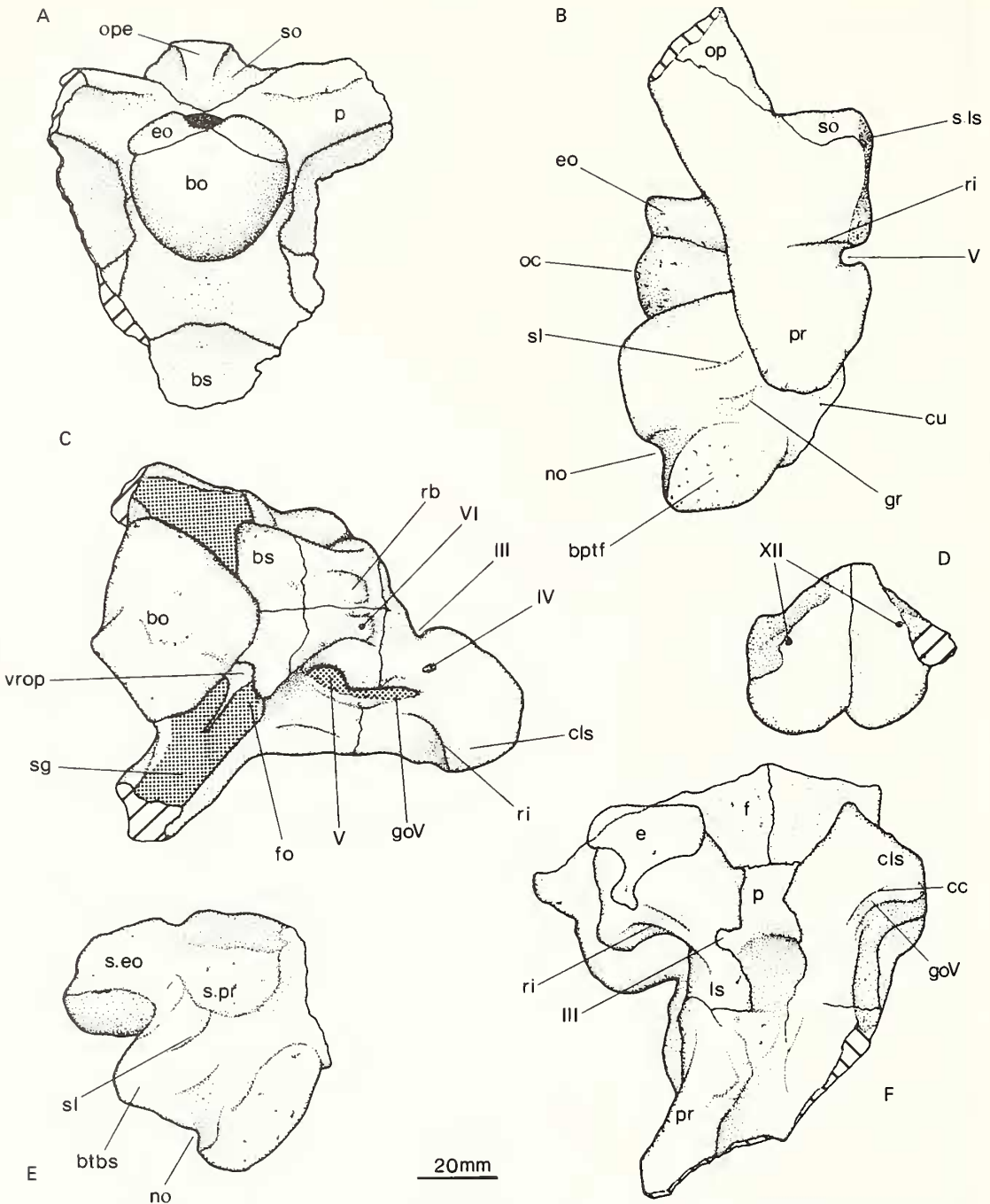
Shansisuchus shansisuchus *Young* (Text-fig 6)

Shansisuchus shansisuchus is an erythrosuchid originally described by Young (1964), from a large amount of material collected from Upper Ehrmaying (Middle Triassic) deposits in China. Young briefly described the braincase only of the paratype IVPP V2501 and figured this and another, unnumbered specimen (field collection 56173). Since this work, the braincase of *S. shansisuchus* has received little further attention. Cruickshank (1970) understood from Young's information that a laterosphenoid was absent. Parrish (1992) scored *S. shansisuchus* for three braincase characters without detailed discussion. Clark *et al.* (1993) noted the apparent presence of a laterosphenoid in Young's (1964) figure 6.

Apart from the two specimens figured by Young (1964), there are, among the paratype material (mostly under field collection no. 56173), at least some further 17 fragmentary specimens, all of which are incompletely prepared. The most complete braincase, belonging to IVPP V2501, has now unfortunately been obscured by plaster, paint, and metal during the course of mounting for display. However, information has been pieced together from the other fragmentary specimens, and a detailed description of the external surface of most of the braincase is now possible. No braincase material has been referred to the other two named species of *Shansisuchus*. In terms of their known morphology, *S. heiyoukouensis* (Young 1964) and *S. kuyeheensis* (Cheng 1980) appear to be indistinct from *S. shansisuchus*.

Basioccipital. The basioccipital is very similar to that of *Erythrosuchus*. It is completely excluded from the floor of the cerebral cavity and foramen magnum. The occipital condyle is directed posteroventrally and the condylar neck is weakly defined. The basal tubera are broad, simple, and diverge quite strongly. They overlap the dorsal part of the basal tubera of the basisphenoid and their posterior surface is shallowly concave. They are not composed of medial and lateral parts as recorded by Parrish (1992, table 2).

Exoccipitals. The exoccipitals are the same as in *Erythrosuchus* in that they meet along the midline on the floor of the cerebral cavity, and their medial margins do not diverge posteriorly on the floor of the foramen magnum. They also meet dorsally (Text-fig. 6A) to exclude the supraoccipital from the border of the foramen magnum. Here the exoccipital bears a simple facet for the proatlas. The exoccipital is indistinct suturally from the opisthotic at the base of the paroccipital process. The posterior surface of the base of the paroccipital process is concave, but this depression is not as marked as that seen in *V. triplicostata*. No specimen currently shows very clearly the area of the exit of the hypoglossal nerve. Two specimens showing the internal area of this exit indicate that there was a single foramen on each side of the braincase (Text-fig. 6D).

TEXT-FIG 6. *Shansisuchus shansisuchus*. Various IVPP braincase specimens; field collection 56173. A, posterior and slightly ventral view of braincase; B, right lateral view of braincase of IVPP V 2511; C, ventral view of crushed braincase; D, dorsal view of isolated exoccipitals; E, right lateral view of isolated basioccipital and basisphenoid; F, ventral view of laterosphenoids and posterior part of skull roof.

Supraoccipital. The supraoccipital is essentially similar to that of *V. triplicostata*, except notably in that it makes a large contribution to the posteriorly projecting occipital peg (Text-fig. 6A), which in *V. triplicostata* is formed solely by the postparietal. The supraoccipital of *Shansisuchus* also forms a small part of the ceiling to the endocranial cavity.

Opisthotic. The opisthotic forms most of the paroccipital process, the distal end of which is incompletely known. the dorsomedial edge of the paroccipital process bears a projection which articulates with a well-defined notch on the ventral edge of the posterolateral process of the parietal. This suggests that the posttemporal fenestra was considerably reduced.

The opisthotic forms the border between the metotic foramen and the fenestra ovalis with a thin lamella of bone, the ventral ramus of the opisthotic. This is similar to that of *Erythrosuchus*, but different to those of *V. triplicostata*, *Fugusuchus* and *Xilousuchus*, in that it is much reduced and does not stand proud of the crista prootica or have a greatly expanded distal end that is visible in lateral and posterior views. Furthermore, there is no indication of an equivalent of the posterior end of the 'pseudolagenar recess' between the ventral ramus and the basal tubera, such as described for the other three taxa above.

Prootic. Posteriorly the prootic forms the anterior surface of the proximal end of the paroccipital process, as shown in Text-figure 6B. The lateral surface of the superior anterior prootic process bears an approximately horizontally aligned brow over the trigeminal foramen. The inferior process resembles that of *Erythrosuchus* more than that of either *V. triplicostata* or *Xilousuchus*, in that the margin of the crista prootica is simple (the specimen in Young's fig. 5 is eroded in this area) and there is no horizontal ridge below the trigeminal foramen. The crista prootica also sheaths laterally the ventral ramus of the opisthotic. Beneath where the inferior process articulates with the laterosphenoid, the prootic bears the depression which houses the exit for the abducens nerve. This area, in *Shansisuchus*, is anteriorly facing (the specimen shown in Text-fig. 6C has been strongly crushed in this area). It is not well preserved and/or prepared in any specimen.

Basisphenoid. The basisphenoid of *Shansisuchus* is a vertically aligned element that is very similar in overall form to that of *Erythrosuchus*. The basal tubera of the basisphenoid are positioned above the oval facets of the comparably sized basipterygoid processes. All of the expected features are present, but they are not well defined. The clinoid process is a low relief feature, and the semilunar depression is only faintly discernible on the lateral surface of the basal tuber. Correspondingly, the lateral groove for the palatine branch of the facial nerve is only weakly incised. This groove widens and deepens posteriorly, to form a broad notch that transmitted the internal carotid artery and facial nerve to the posteroventral surface of the basisphenoid.

The posterior surface of the basisphenoid is poorly known because of the incomplete preservation and preparation of a number of specimens. The dorsal part is substantially overlapped by the tubera of the basioccipital (Text-fig. 6A), and immediately ventral to this is the least well known area of the basisphenoid. The lack of a well preserved and/or prepared posterior basisphenoid surface means that there is currently no evidence for the presence of an intertuberal plate (*contra* Parrish 1992). The paired foramina for the internal carotid arteries are situated on the posteroventral surface, beneath a ridge of bone and close to the notches between the basal tubera and basipterygoid facets.

The suturally indistinct parasphenoid of *Shansisuchus* is unknown except for the laterally compressed base of the cultriform process. It is remarkably tall, with the dorsal part being overlapped by the crista prootica and the ventral edge extending below the dorsal margin of the basipterygoid facet (Text-figs 6B, E).

Laterosphenoid. There has been much uncertainty over the presence of a laterosphenoid ossification in the braincase of *Shansisuchus*, perhaps because of the lack of first-hand information. The paratype material, however, includes several specimens which confirm its expected presence. It still remains poorly known, with the best examples currently being two incomplete and strongly crushed specimens (Text-figs 6C, F).

The laterosphenoid is very similar to that of *V. triplicostata* and *Erythrosuchus*, particularly in being of robust construction. The capitate process is particularly thick and there is a strong ridge running up its lateral edge. The anterior process is incomplete in both specimens, but does not appear to have been either long or slender. Because of compression and erosion it is not possible to assess the possibility of the presence of an 'anterodorsal channel' between the capitate and anterior processes, such as is seen in *V. triplicostata* and *Erythrosuchus*. The anteromedial margin is the least well preserved part of these two specimens, so that the location of an exit foramen for cranial nerve II has not been positively identified. A well-defined notch seen in the medial margin of the laterosphenoid and near the laterosphenoid-prootic suture, was probably for the

passage of cranial nerve III. The only sign of a possible exit foramen for cranial nerve IV is an incompletely prepared pit on the anteroventral surface of the specimen illustrated in Text-figure 6G. A groove immediately posterior to the weakly defined cotylar crest probable carried the opthalmic branch of the trigeminal nerve. The posterior end of this groove is deeply incised, so that the unprepared trigeminal foramen appears to be long, narrow, and formed by the laterosphenoid as well as the prootic (Text-fig. 6C).

PHYLOGENETIC IMPLICATIONS

The taxa and characters

The descriptions above give an indication of several braincase characters that might be of use in a study of early archosaur phylogeny. A preliminary attempt was made to investigate the phylogenetic informativeness of braincase morphology by constructing a data matrix of phylogenetic characters for representative early archosaur taxa. The selected taxa were those that have adequately known braincase material. Three crown-group archosaurs were selected, based on the criterion of availability of detailed, published braincase descriptions. *Prolacerta* was included as a non-archosaurian representative.

The 11 taxa used (with the sources of the information, where not only from our own observations, given in parentheses) are: *Prolacerta* (Gow 1975; Evans 1986); *Proterosuchus* (Cruickshank 1970, 1972; Gow 1975; Clark *et al.* 1993); *Fugusuchus* (Cheng 1980); *Xilousuchus; Vjushkovia triplicostata; Erythrosuchus; Shansisuchus; Euparkeria* (Cruickshank 1970, 1972; Evans 1986; pers. obs. of UMCZ T692); *Sphenosuchus* (Walker 1990); Parasuchia (Camp 1930; Chatterjee 1978); *Stagonolepis* (Walker 1961, 1990, pers. comm.).

Characters were selected on the basis of informativeness with respect to the taxa employed. The definition of states of the 17 characters that were deemed suitable are listed below.

Characters included in analysis. These are included on the criteria of an informative distribution of character states among the taxa included, as well as discrete states being clearly recognizable.

1. Position on basisphenoid of foramina for the cerebral branches of the internal carotid arteries leading to the pituitary fossa (ventral/posteroventral = 0; lateral = 1). The plesiomorphic condition for archosaurs is for the internal carotid foramina to be in a ventral (e.g. *Prolacerta, Proterosuchus*) or posteroventral (*V. triplicostata*) position, on the external surface of the braincase. The posteroventral position is also seen in *Euparkeria* (pers. obs. of UMCZ T692). The foramina in more derived archosaurs (e.g. *Stagonolepis* Walker 1961; Parrish 1993; *Postosuchus* Chatterjee 1985; *Parasuchus* Chatterjee 1978; *Massospondylus* Gow 1990) are positioned on the lateral surface of the basisphenoid. Parrish (1993, character 7) appears to have been the first to use this character in reconstructing basal archosaur phylogeny. However, the scoring of this character by Parrish (1993, table 2) for many of his included taxa is contradicted by his discussion in the text (1993, p. 289), and by his comment that a lateral position of the foramina is a synapomorphy of proterochampsids + crown-group archosaurs (*Euparkeria* is incorrectly scored as exhibiting the lateral position; *Chanaresuchus, Erythrosuchus, Proterosuchus*, and all crown-group archosaurs except *Riojasuchus* are scored as exhibiting the posteroventral position). In the plesiomorphic condition, the proximity of these paired foramina to the midline shows some variation and may also be phylogenetically informative.
2. Basisphenoid intertuberal plate (present = 0; absent = 1). The presence of a plate between the basal tubera of the basisphenoid was interpreted by Parrish (1992) as an erythrosuchid synapomorphy. It has been shown above that this plate is apparently homologous with one present on the horizontally aligned basisphenoids of, for example, *Prolacerta, Proterosuchus*, and *Fugusuchus* (correctly scored by Parrish). The state is currently unknown in *Shansisuchus*. In *Erythrosuchus* and *Xilousuchus* the plate is present as a much reduced feature. Equivalent structures have yet to be identified in other archosaur taxa, including *Euparkeria*.
3. Elements enclosing abducens foramen (basisphenoid and prootic = 0; within prootic only = 1). In early archosaurs and immediate outgroups, such as *Euparkeria, Proterosuchus* and *Prolacerta*, the external foramina for the abducens nerves lie between the basisphenoid and prootics. This is also the case in some more derived archosaurs such as *Parasuchus* (Chatterjee 1978). In *Erythrosuchus, V. triplicostata, Xilousuchus*, and *Shansisuchus*, however, the external abducens foramina are held entirely within the prootic. An additional state of 'abducens foramina within basisphenoid only', could be added, but in this analysis would be uninformative as it is seen only in *Sphenosuchus* (Walker 1990). The relationship of this third state to the others is uncertain

and so *Sphenosuchus* is coded as equivocal in this analysis. In *Erythrosuchus*, the internal exit foramen for the abducens nerve is also held entirely by the prootic, while in *V. triplicostata* this lies between basisphenoid and prootic. 'External abducens foramina held by prootic only' may therefore be an erythrosuchid synapomorphy, with *V. triplicostata* retaining the plesiomorphic condition internally.

4. Position of external abducens foramina (on an anterior = 0; or ventral = 1 surface). In *Prolacerta*, *Proterosuchus*, and *V. triplicostata*, the external abducens foramina are positioned on the horizontal ventral surface of the inferior anterior prootic process. In *Erythrosuchus*, *Shansisuchus*, and some non-erythrosuchid archosaurs, such as *Parasuchus* and possibly *Euparkeria*, the external exit foramina for the abducens nerves lie on a vertical, upturned anterior surface of the front of the braincase.

5. Ventral ramus of the opisthotic (prominent = 0; recessed = 1). In immediate archosaur outgroups, as well as *Proterosuchus*, *Euparkeria*, *Fugusuchus*, *Xilousuchus* and *V. triplicostata*, the lamellar part of the ventral ramus of the opisthotic is very prominent, making it clearly visible in lateral and posterior views. In *Erythrosuchus* and *Shansisuchus*, the ventral ramus is poorly developed and does not stand proud of the stapedial groove. The ramus is also reduced in phytosaurs (Camp 1930; Chatterjee 1978), but it is not recessed within a deep stapedial groove, and remains visible in lateral view.

6. Ridge on lateral surface of inferior anterior prootic process below trigeminal foramen (present = 0; absent = 1). The presence of this feature has been described above in *V. triplicostata*, *Fugusuchus* and *Xilousuchus*. It can also be seen in immediate archosaur outgroup taxa, such as *Hyperodapedon* (Benton 1983) and *Prolacerta* (Gow 1975). It is perhaps the dorsalmost part of the area of origin of the protractor pterygoidei, such as in the extant taxon *Ctenosaura* (Oelrich 1956, p. 45, fig. 35).

7. Basisphenoid (horizontally = 0; or more vertically = 1 oriented). *Prolacerta*, *Proterosuchus*, and *Fugusuchus* all have a horizontally aligned basisphenoid. Erythrosuchids, *Euparkeria*, and a range of more derived archosaurs show some degree of verticalization of this element, with the basipterygoid processes positioned ventral as well as anterior to the basal tubera. The condition in phytosaurs is difficult to interpret from published figures. The presumably plesiomorphic condition (horizontal) is apparently retained/reversed in some derived archosaurs (e.g. *Massospondylus* Gow 1990, *Lewisuchus* Romer 1972 and birds Chatterjee 1991).

8. Crista prootica outline (simply curved = 0; sinusoidal = 1). Most early archosaur taxa exhibit a regular and simply curved free edge to the crista prootica as seen in lateral view. *V. triplicostata* and *Xilousuchus*, as described above, show a sinusoidally curved edge.

9. Prootic midline contact on endocranial cavity floor (absent = 0; present = 1). Evans (1986) pointed out that archosaurian outgroup taxa such as *Prolacerta* and rhynchosaurs lack any midline contact between the opposite prootics on the endocranial cavity floor. *Erythrosuchus*, *V. triplicostata*, *Shansisuchus*, and probably *Xilousuchus*, all exhibit such contact.

10. Basisphenoid midline exposure on endocranial cavity floor (present = 0; absent = 1). In the majority of taxa studied, the absence of midline exposure of the basisphenoid on the floor of the endocranial cavity is consistently linked with the presence of prootic midline contact. The condition seen in *Parasuchus* (Chatterjee 1978), however, shows that these two features do not always coincide. The plesiomorphic condition, as seen in e.g. *Hyperodapedon* (Benton 1983), is apparently the presence of midline basisphenoid exposure.

11. Semilunar depression (present = 0; absent = 1). The groove, currently of unknown function, described on the lateral surface of the basal tubera of the basisphenoid of *Prolacerta*, was termed 'semilunar depression' by Evans (1986). An apparently homologous groove has been found in the taxa described above, and is also present in *Erythrosuchus*, *Proterosuchus* (Gow 1975, fig. 25), and *Euparkeria* (pers. obs. of UMCZ T692). The apparent absence of this feature in extant diapsids means that discovering the function of this feature is currently extremely problematical. This does not, however, prevent it from being a potentially informative feature for phylogenetic analysis.

12. Laterosphenoid anterodorsal channel (absent = 0; present = 1). The anterodorsal channel, seen between the anterior and capitate processes of the laterosphenoid and the parietal in *Erythrosuchus* and *V. triplicostata* is currently of unknown function. It is absent in *Proterosuchus* but unknown in the other early archosaurs considered here. Whatever its function, its position and form might currently be interpreted as a synapomorphy of a group including, at least, *Erythrosuchus* and *V. triplicostata*.

13. Parasphenoid cultriform process (simple = 0; dorsoventrally constricted towards the base = 1). In lateral view, the base of the cultriform process of the parasphenoid may be constricted, before expanding slightly and eventually tapering anteriorly. This is seen in *Proterosuchus* (Cruickshank 1972) and *Fugusuchus* (see above), but not in *Prolacerta* (Gow 1975) or *Xilousuchus* (see above). Unfortunately this area is not well preserved in a number of other early archosaurs.

14. 'Pseudolagenar recess' between ventral surface of the ventral ramus of the opisthotic and the basal tubera (present = 0; absent = 1). This channel is of unknown function. Its anterodorsal limit, in *V. triplicostata*, is

seen to be in a position approximately relating to that where an ossified lagenar recess might be found. However, the posterior continuation of this channel between at least three elements, and the fact that it is closed in closely related taxa, suggests that a more plausible interpretation is that it represents an area of residual cartilage. An unossified gap is also seen between braincase elements in, for example, extant and extinct sphenodontians (Wu 1994). The 'pseudolagenar recess' is seen in *Prolacerta* (Gow 1975, fig. 34), *Proterosuchus*, *Euparkeria* (pers. obs. of UMCZ T692), *V. triplicostata*, *Fugusuchus*, and *Xilousuchus*. The absence of this channel in *Erythrosuchus* and *Shansisuchus*, or at least its not opening externally, would seem to be paralleled in more derived, crown-group archosaurs.

15. Base of cultriform process of parabasisphenoid (relatively short dorsoventrally = 0; tall, with the dorsal edge extending up between clinoid processes and ventral part of cristae prootica = 1). In *Prolacerta*, the base of the cultriform process is not tall and does not extend up between the anterior edges of the clinoid processes of the basisphenoid. This condition is seen also in *V. triplicostata*, *Fugusuchus* and *Xilousuchus*. In *Shansisuchus* and *Erythrosuchus*, the base of the cultriform process is proportionately much taller, and the dorsal edge extends up between the clinoid processes. The latter condition is also seen in crown-group taxa including *Machaeroprosopus* (Camp 1930) and *Stagonolepis* (Walker 1961). We also consider it to be present in *Sphenosuchus*, although the parabasisphenoid as a whole is much derived over that seen in earlier archosaurs.

16. Number of hypoglossal foramina (two = 0; one = 1). While all of the taxa described above have only a single foramen for the hypoglossal nerve, this is not the condition present in all archosauromorph taxa. Two foramina are not uncommon and have been reported in *Euparkeria* (Cruickshank 1970), *Paradapedon* (Chatterjee 1974), *Parasuchus* (Chatterjee 1978), *Hyperodapedon* (Benton 1983), *Prolacerta* (Evans 1986) and *Sphenosuchus* (Walker 1990). Extant crocodilians have been one and three foramina (Iordansky 1973).

17. Medial margin of exoccipitals (do not make contact = 0; make contact for majority of their length = 1; meet anteriorly, but diverge posteriorly = 2). In *Prolacerta* (Gow 1975; Evans 1986), the opposite exoccipitals do not make contact along the midline of the braincase floor, allowing exposure of the basioccipital here. This is also the condition in a number of relatively derived archosaurs (e.g. living crocodilians, Iordansky 1973; *Sphenosuchus*, Walker 1990). In all of the taxa described above, as well as in *Erythrosuchus*, the exoccipitals make substantial contact along the midline to prevent exposure of the basioccipital on the braincase floor. Midline exoccipital contact is also seen in *Parasuchus* (Chatterjee 1978).

In *Prolacerta*, and also in archosaur outgroup taxa where the exoccipitals meet along the midline (e.g. *Hyperodapedon* Benton 1983), the medial margins of the exoccipitals are parallel to one another. In *V. triplicostata*, *Fugusuchus* and *Xilousuchus*, the posterior part of the medial exoccipital margins diverge to expose the dorsal surface of the basioccipital.

Although the divergence of the medial margins of the exoccipitals is possibly logically independent from the presence of midline contact, lack of contact and divergence are not known to occur together. Treating this as two separate binary characters (presence/absence of contact; presence/absence of posterior divergence) would effectively order the acquisition of the derived states (0-1-2) of the character defined here. Further investigation of this character may shed some light on its possible association with other characters. *Hyperodapedon*, for example, exhibits midline exoccipital contact but also anteroventral exposure of the basioccipital (Benton 1983).

Several potential characters were removed from the analysis *a priori*, either because they are uninformative in the context of this preliminary analysis, or because they are problematical in terms of recognizing discrete states.

Uninformative characters. These include characters with an uninformative distribution of states among the taxa included in this analysis (at least one of their states present in fewer than two taxa), as well as characters that are here interpreted as autapomorphic for particular early archosaurs. Only those characters of relevance to the earliest archosaurs are discussed here.

18. Presence of a laterosphenoid. The presence of an ossified laterosphenoid was formerly thought to be a synapomorphy only of the crown-group archosaurs, but Clark *et al.* (1993) have shown it to be present in all archosaurs (their Archosauriformes). Disarticulation of the laterosphenoid from the rest of the braincase is apparently common in early archosaurs (see above and Clark *et al.* 1993), making it difficult to confirm the absence of this element in specimens represented by disarticulated cranial remains. This character is uninformative in the present analysis because only *Prolacerta* is known to lack a laterosphenoid.

19. Laterosphenoid-postorbital contact. This contact is present in the crown-group archosaurs employed in

this analysis, as well as in *Erythrosuchus* and possibly *V. triplicostata*. *Proterosuchus*, however, is the only taxon in this analysis known to lack laterosphenoid-postorbital contact (Clark *et al.* 1993).

20. Epipterygoid articulation. The epipterygoid articulates with the skull roof in *Proterosuchus* (Clark *et al.* 1993), but with the laterosphenoid in, for example, *Parasuchus* (Chatterjee 1978) and possibly *Erythrosuchus*. The use of this character, however, relies on the discovery of well-preserved and articulated material and in the present analysis the condition is known with certainty only for the Parasuchia.

21. Supraoccipital contribution to occipital peg. In erythrosuchids there is a free-standing and conical posterior peg formed by the postparietal. In *Shansisuchus* and *Vjushkovia sinensis* (DJG, pers. obs.), this peg is formed in part by the dorsal edge of the supraoccipital. The absence of *V. sinensis* in this analysis means that this feature is present only in *Shansisuchus* among the included taxa.

22. Basal tubera of the basioccipital. While Parrish (1992) was mistaken in his identification of separate lateral and ventral components to the basal tubera in a number of erythrosuchid taxa (see above), certain taxa do exhibit bilobed tubera. These include *Xilousuchus* (see above) and *Dorosuchus* (Sennikov 1989). This character is excluded because bilobed tubera are known in only a single taxon (*Xilousuchus*) included in the present analysis.

23. Presence of a medial tubercle projecting ventrally from between the basal tubera of the basioccipital. This is currently interpreted as an autapomorphy of *V. triplicostata*.

24. Anterodorsal end of the trigeminal foramen. In *Shansisuchus*, the anteriodorsal end of the trigeminal foramen appears to be narrow and extending onto the laterosphenoid. This is currently interpreted as a possible autapomorphy of *Shansisuchus*.

Problematical characters. These are deemed to be unsuitable because of poor current knowledge, variability within terminal taxa, or absence of satisfactorily definable states.

25. Fusion of opisthotic-exoccipital. The exoccipital and opisthotic are seen externally as suturally distinct elements in, for example, *Hyperodapedon* (Benton 1983), *Prolacerta* (Gow 1975; Evans 1986) and *Euparkeria* (Cruickshank 1970), but not in any of the taxa described above. The presence of fusion has been considered apomorphic for archosaurs (e.g. Benton and Clark 1988), or as having an equivocal distribution (Sereno and Arcucci 1990). It is assumed that the previous use of this character, though not explicitly defined, applies to the external, occipital surface of these elements, particularly at the base of the paroccipital process. Sutures between these elements can often be seen on the internal surface of the braincase, in or near the vestibule, even when the two elements appear to be fused in external views. Use of this character is eurrently hampered by the lack of descriptive information, unclear reconstructions, and ignorance about the possible ontogenetic effects. For example, Chatterjee (1974) does not describe, but reconstructs, *Paradapedon* as having a fused exoccipital-opisthotic and the condition is unclear for *Proterosuchus* based on the information presented by Gow (1975) and Cruickshank (1972). Furthermore, the use of this character may often rely on the availability of particularly well preserved material. It is here considered to currently be too poorly understood to be included in this phylogenetic analysis.

26. Anterior process of laterosphenoid. *Proterosuchus* has long and slender anterior laterosphenoid processes (Clark *et al.* 1993) and *Erythrosuchus* has short processes, while *V. triplicostata* represents something of a morphological intermediate. Information is unfortunately lacking for the laterosphenoids of a number of the earliest archosaurs, so that currently this character is of little use. Furthermore, it may be a strongly 'sliding scale' character, presenting problems for the identification of discrete character states.

27. Laterosphenoid thickness. The laterosphenoid of the earliest archosaurs is a thick bone, differing from the thin-walled homologue in, for example, modern crocodilians. This character needs further investigation based on disarticulated material, although objective recognition of discrete states might be problematical.

28. Fossae for retractor bulbi eye muscles. In all of the taxa described above, as well as in *Erythrosuchus* and *Euparkeria* (Gow 1975), the abducens foramina are positioned within a pair of fossae that are probably for the retractor bulbi eye muscles. These fossae are clearly separate from the pituitary fossa. In the archosaur outgroup taxa *Hyperodapedon* (Benton 1983), and apparently *Prolacerta* (Evans 1986), the abducens foramina lie a significant distance above the retractor fossae. This is also the condition in the extant lizard *Varanus* (Säve-Söderbergh 1946). It might be noted, however, that the abducens foramina do appear to be within the fossae in the extant taxa *Ctenosaura* (Oelrich 1956) and *Sphenodon* (Säve-Söderbergh 1946). Lack of further available information, particularly for early archosaurs, currently prevents a conclusive assessment of this character.

29. Middle cerebral vein exit. *Stagonolepis* (Walker 1990) exhibits a foramen for the exit of the middle cerebral vein that is separate to that for the trigeminal foramen. Other taxa, including *Ctenosaura* (Oelrich 1956) and *Sphenosuchus* (Walker 1990), may exhibit a partial separation of nerve and vein foramina, while most early

TABLE 1. Braincase character states for selected early archosaurs and *Prolacerta*. Characters are discussed in the text.

Taxa	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Prolacerta	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Proterosuchus	0	0	0	0	0	0	0	?	?	?	0	0	1	0	0	?	?
Fugusuchus	0	0	?	0	0	0	0	0	?	?	0	?	1	0	0	1	2
Xilousuchus	0	0	1	0	0	0	1	1	1	?	0	?	0	0	0	1	2
V. triplicostata	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	2
Erythrosuchus	0	0	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1
Shansisuchus	0	?	1	1	1	1	1	0	1	?	0	1	0	1	1	1	1
Euparkeria	0	1	0	1	0	0	1	?	?	?	0	?	1	0	0	0	0
Sphenosuchus	1	1	?	1	0	1	1	0	0	0	1	0	0	1	1	0	0
Parasuchia	1	1	0	?	0	1	?	0	1	0	1	0	?	1	1	0	1
Stagonolepis	1	1	?	?	0	1	1	0	?	?	1	?	?	1	1	0	?

archosaurs show no indication of any such separation. This is another character requiring further investigation and well-preserved material before a full assessment can be made. For example, *Proterosuchus* may not have a simple trigeminal foramen (Clark *et al.* 1993, fig. 2), but whether this is a real and consistent feature and/or indicative of an ossified separation of the nerve and vein is uncertain.

30. Supraoccipital. The amount of supraoccipital contribution to the border of the foramen magnum is seen to vary in archosaurs and their outgroups. For example, the supraoccipital forms some of the foramen magnum in *Paradapedon* (Chatterjee 1974), *Hyperodapedon* (Benton 1983), *Sphenosuchus* (Walker 1990), and *Parasuchus* (Chatterjee 1978), but not in any of the taxa described above. The informativeness of this character, however, is called into question by information presented by Evans (1986), who reported that *Prolacerta* is polymorphic for this character.

31. Posttemporal fenestra. This is highly reduced in *Erythrosuchus*, *Shansisuchus* and *V. triplicostata*, in which a projection on the dorsal edge of the paroccipital process articulates intimately with a concavity of the ventral surface of the parietal. *Fugusuchus* and *Proterosuchus* may lack this type of paroccipital-parietal articulation, but the posttemporal fenestra is also reduced (Cruickshank 1970, 1972; Cheng 1980). A relatively large fenestra is seen in the archosaur outgroup taxa *Prolacerta* (Gow 1975), *Paradapedon* (Chatterjee 1974) and *Hyperodapedon* (Benton 1983). There are problems with this character, both in defining discrete states and in assessing the size of the fenestra without the availability of well-preserved and articulated material. The extent of the fenestra in *Xilousuchus*, for example, is difficult to assess.

32. Slender process of the laterosphenoid. This process is a slender, ventral extension of the area separating the notches for the passage of cranial nerves II and III. To date, it has been described only in *Proterosuchus* (Clark *et al.* 1993), although it is possibly also present in *Euparkeria* (Clark *et al.* 1993).
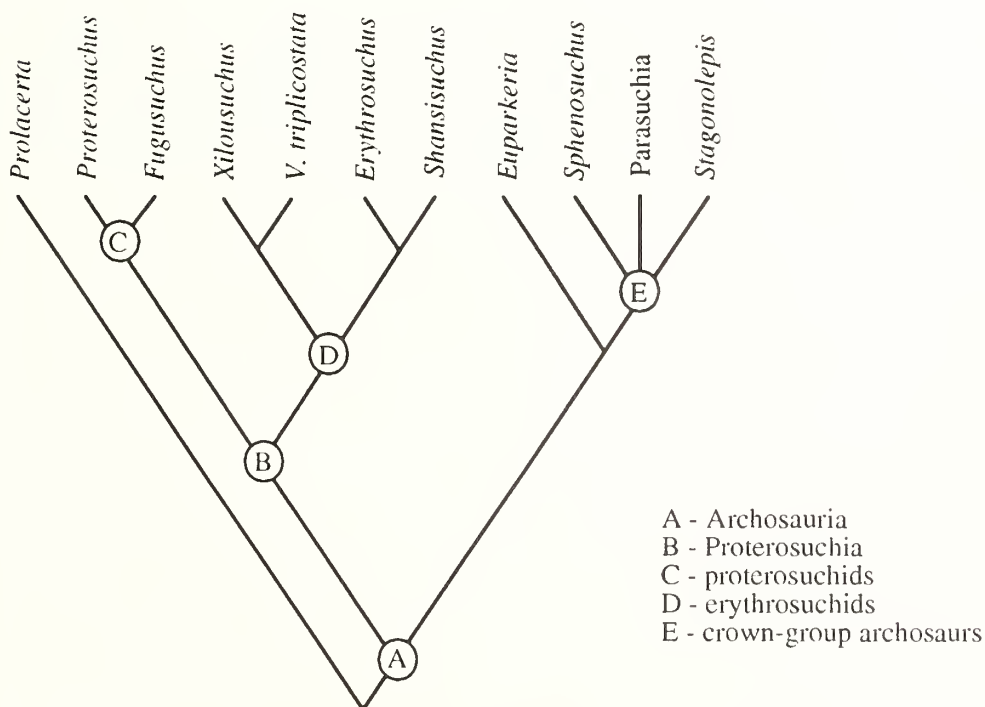
Phylogenetic analysis

A data matrix for the 11 taxa and 17 informative characters discussed above is shown in Table 1. The data were analysed using permutation tests and parsimony.

Permutation. Two permutation tests were performed on the data as presented in Table 1. The results of permutation tests produce quantifiable measures of 'phylogenetic structure' within a given data set. The first measure applied to the data was the permutation tail probability (PTP) test (Archie 1989; Faith and Cranston 1991), a measure of the probability that a random data set would yield an equally parsimonious tree. PERMUTE (Wilkinson 1992a) was used to generate randomly permuted data sets, and to summarize the results of their analysis using Hennig86 (Farris 1988). Equal character weighting was employed and 99 random data sets were generated. This produced a result of PTP = 0·01, whether or not *Prolacerta* was included.

The second permutation test used was the character compatibility permutation tail probability (CCPTP) of Wilkinson (1992b), which is equivalent to the test statistic 'C' of Alroy (1994). This test measures the probability that a random data set would yield an equal level of character compatibility, i.e. whether or not the data set contains significant hierarchical structure (Alroy 1994). The data were analysed, with equal character weighting and 999 random data sets, using the program PICA (Wilkinson 1995). This produced a result of CCPTP = 0·0001, whether or not *Prolacerta* was included.

The results of both the parsimony-based and compatibility-based permutation tests represent the minimum possible values (given the number of random data sets employed), allowing us to reject confidently the null hypothesis that the real data do not differ significantly from random. The non-randomness is not just based on differences between the in- and outgroup, as shown by the minimum PTP and CCPTP values obtained even when *Prolacerta* was excluded. While recognizing that both of the methods used here are not without drawbacks (Alroy 1994), we conclude that these braincase data exhibit significant hierarchical structure, which is interpreted as the result of phylogeny.

Parsimony. Parsimony analysis of the data presented in Table 1 was carried out using PAUP (version 3.1.1, Swofford 1992) on a Macintosh LC computer. Searches were performed using the branch and bound option. All characters were equally weighted and unordered, and trees were rooted with the outgroup *Prolacerta*. The search yielded a single most parsimonious tree (MPT) of length (L) 26 steps with a consistency index (CI) of 0·692 and a retention index (RI) of 0·81. This tree is shown in Text-figure 7.
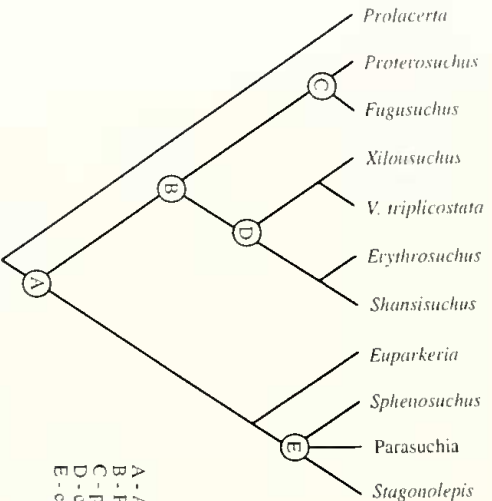

TEXT-FIG 7. Most parsimonious hypothesis of the relationships of selected early archosaurs based only on data (Table 1) from braincase morphology.

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TEXT-FIG. 7. Most parsimonious hypothesis of the relationships of selected early archosaurs based only on data (Table 1) from braincase morphology.

A - Archosauria
B - Proterosuchia
C - proterosuchids
D - erythrosuchids
E - crown-group archosaurs

Prolacerta
Proterosuchus
Fugusuchus
Xilousuchus
V. triplicostata
Erythrosuchus
Shansisuchus
Euparkeria
Sphenosuchus
Parasuchia
Stagonolepis

Prolacerta aside, there are two main clades: *Euparkeria* plus the crown-group archosaurs, and the proterosuchians. The relative position of *Euparkeria* with respect to the crown-group and proterosuchian taxa agrees with the most recent studies of archosaur phylogeny (Benton and Clark 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1993). Two main clades can be recognized within the proterosuchians: the erythrosuchids (*Erythrosuchus*, *Shansisuchus*, *V. triplicostata*, *Xilousuchus*) and the proterosuchids (*Proterosuchus + Fugusuchus*). These particular hypothesized relationships are contrary to previous cladistic studies of the relationships of the earliest archosaurs (e.g. Benton and Clark 1988; Sereno 1991; Parrish 1992), all of which hypothesized that the Proterosuchia is a paraphyletic grade. The hypothesis presented in Text-figure 7 also contradicts existing views on more detailed aspects of early archosaur relationships. Recently, in the only cladistic analysis to look in any detail at the earliest archosaurs, Parrish (1992) postulated that *Fugusuchus* is an erythrosuchid rather than a proterosuchid, but the result obtained here supports Cheng's (1980) original diagnosis. *Xilousuchus*, although never before included in a cladistic analysis, was originally identified by Wu (1981) as a proterosuchid. Within the Erythrosuchidae, Parrish (1992) postulated that *Erythrosuchus* lies outside the most derived erythrosuchid clade of *Vjushkovia + Shansisuchus*.

The presence of the two holophyletic groups composed of *Shansisuchus + Erythrosuchus* and *V. triplicostata + Xilousuchus* (Text-fig. 7), is predictable from an examination of Table 1. *Shansisuchus* shares exactly the same character distributions as recorded for *Erythrosuchus*, except for two characters (2, 10) which are missing values for the former taxon. Because *Erythrosuchus* has no missing data in this analysis, *Shansisuchus* and *Erythrosuchus* are potential taxonomic equivalents exhibiting a 'one way asymmetrical' distribution of missing values (Wilkinson 1992b). There can, therefore, be no more parsimonious interpretation of the relationships of *Shansisuchus* than its origin from the same node as *Erythrosuchus*. A similar situation is also seen with *V. triplicostata* and *Xilousuchus*. Indeed, *Shansisuchus* and *Xilousuchus* (because they have more missing data than their respective potential equivalents) could have been safely deleted from the analysis *a priori*, without affecting the parsimonious interpretation of the relationships of the remaining taxa (Wilkinson 1992b; Wilkinson and Benton 1995). Incidently, a character compatibility permutation test performed on the data set in Table 1 without *Shansisuchus* and *Xilousuchus* still produces minimum possible CCPTP and PTP values of 0·001 and 0·01 respectively (based on 999 and 99 random data sets respectively.

In summary, while the general structure of the cladogram in Text-figure 7 agrees with previously published analyses of basal archosaur phylogeny (*Euparkeria* is a sister group to the crown-group archosaurs; Erythrosuchidae and Proterosuchidae are holophyletic), some details are in conflict.

Additional parsimony analyses were performed with the aim of making a brief investigation of the robustness of the initial hypothesis. Various combinations of taxa presented in Table 1 were selected for re-analysis. As taxa were deleted, the number of informative characters rapidly reduced and the number of MPTs often increased. For example, excluding the crown-group archosaurs and the taxonomic equivalents *Xilousuchus* and *Shansisuchus*, left only six characters (3–4, 7, 13, 16–17) that remained informative for the six remaining taxa. PAUP analysis of this restricted data set produced five MPTs of L = 10; CI = 0·7; RI = 0·625. In these trees, *Proterosuchus* appears in a clade with *Euparkeria*, in a clade with *Fugusuchus*, as the sister group to *Fugusuchus* plus the erythrosuchids, as the sister group to *Euparkeria* plus the erythrosuchids and, finally, as the sister group to the erythosuchids with *Fugusuchus* and *Euparkeria* lying outside this clade. If *Prolacerta* is subsequently removed, only four characters (3–4, 7, 13) are informative in a restricted data set including five taxa.

We investigated also the effect that the inclusion of *Prolacerta* might have on the hypothesized relationships of basal archosaurs. This was achieved by removing only *Prolacerta* from the original data set. Character 9 then became uninformative and was also removed. A PAUP analysis yielded a single MPT (L = 23; CI = 0·739; RI = 0·838). Lundberg rooting of this network, with the

character states observed in *Prolacerta* employed as the ancestral condition, produced the same ingroup relationships as presented in Text-figure 7. The inclusion of *Prolacerta*, therefore, does not perturb the parsimonious interpretation of relationships of the early archosaur taxa used in this analysis.

Finally, various topological constraints were employed to investigate the robustness of the relationships presented in Text-figure 7. Trees with *Fugusuchus* as a member of a holophyletic Erythrosuchidae, or with a paraphyletic Proterosuchia are only one step longer than the original MPT (L = 27). The shortest tree lacking a holophyletic Erythrosuchidae (*Xilousuchus* and *V. triplicostata* lying outside a clade comprising *Erythrosuchus*, *Shansisuchus* plus the crown-group archosaurs) is only two steps longer (L = 28).

These additional results are important in assessing the confidence we might have in the parsimonious interpretation of relationships based on braincase data. The brief investigation of restricted subsets of the original data shows that the relationships indicated in Text-figure 7 are generally supported, irrespective of the removal of some taxa and a large number of accompanying uninformative characters. The analyses performed employing topological constraints indicate that most of the relationships seen in Text-figure 7 that contradict those proposed in the recent literature (see above), are not supported in trees that are only one additional step in length. It should also be remembered that many taxa, and some characters, were excluded *a priori* because of a lack of available data. The inclusion of these data, and other cranial and postcranial characters, may significantly affect the interpretation of relationships. While raising some interesting questions that deserve further investigation, proterosuchian monophyly for example, the relationships seen in Text-figure 7 should certainly not be taken as a definitive view of early archosaur phylogeny.

Finally, we will comment briefly on the level of homoplasy in these braincase data. Parrish (1993, p. 304) has recently suggested that archosaurian braincase features may yield more informative phylogenetic data than some other cranial features obtained from taxa which share superficially similar, carnivorously adapted skulls. That braincases are relatively conservative in their evolution and less prone to convergences occurring through functional requirements, such as feeding mode, is perhaps a widely held, though rarely explicitly stated, view (though see e.g. Gow 1975, p. 118). The instability of the hypotheses discussed here, and the unremarkable CI levels obtained (seven of the 17 characters had a CI of 0·5 in the MPT), cannot be considered to support an hypothesis that archosaurian braincase morphology represents a source of especially informative phylogenetic data. However, we accept that the restricted range of taxa and methods employed here leave considerable room for further investigation.

While the levels of homoplasy in the data indicate that the early archosaur braincase is not exempt from evolutionary convergences, a closer inspection of the character state transformations required by the most parsimonious phylogenetic hypothesis raises some interesting points. Of the eight homoplastic characters, four (4, 6, 14–15) are probably best explained by the convergent acquisition of states in *Erythrosuchus + Shansisuchus* and non-proterosuchian archosaurs, and a further one (7) in all erythrosuchids and non-proterosuchian archosaurs. Of the remaining homoplastic characters, two (9, 17) can be considered as convergences in the pattern of sutural contact on the floor of the endocranial cavity between erythrosuchids and parasuchians, while the last (13) is the probably convergent acquisition of a constricted base to the parasphenoid rostrum in proterosuchids and *Euparkeria*. Although homoplasy is usually viewed as the bane of phylogeny reconstruction, it should be remembered that it is an over-simplification to perceive it merely as misleading evidence, particulary when a distinction between sister group and non-sister group homoplasy is made (Wilkinson 1991). For example, the four features shared by *Erythrosuchus* and *Shansisuchus* that are considered to have been acquired convergently in some non-proterosuchian archosaurs might be considered to be an important part of the evidence supporting the hypothesis that these two erythrosuchids are sister taxa, despite the homoplastic nature of these characters across the data set as a whole. It is also of interest to look at the character transformations implied by the most parsimonious hypothesis from another perspective. For example, a division of the characters into loosely defined categories reveals that those concerning the number and position of

braincase foramina (1, 3, 12, 16) show no homoplasy, while those associated with shape changes (4, 7, 13, 15) all have a CI of 0·5. We are obviously reluctant to make any sweeping conclusions based on this preliminary and rudimentary investigation of the complex question of homoplasy and character informativeness, but believe that it highlights some areas for future work that will be of interest from a functional and evolutionary perspective as well as a purely phylogenetic one.

Braincase data as a whole does not appear to be a panacea for the reconstruction of early archosaur phylogeny. Rather, we suggest that progress will be made in our understanding of both the morphology and relationships of early archosaurs by investigating all regions of the skeleton in greater detail, and by carefully exploring the phylogenetic information that their morphology may yield. The results presented here represent but a small initial step.

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